OLD WORLD MONKEYS

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Old World monkeys: three decades of development and change in the study of the Cercopithecoidea

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Introduction

In 1969, John and Prue Napier brought together researchers from a variety of fields with the intention of examining the systematics of a relatively neglected primate taxon – the Old World monkeys. After a week of intensive discussion, the revised presentations were collated and published in 1970 as *Old World Monkeys: Evolution, Systematics, and Behavior* (henceforth "OWM I"). The conference was noteworthy in that it marked a new phase in the study of the cercopithecoid monkeys, as a taxon meriting detailed attention in its own right.

The present volume was conceived as a tribute to the initiators and editors of OWM I, now, sadly, both deceased. We have aimed to bring together a collection of papers to exemplify important, currently active areas of research on cercopithecoid monkeys. Every scientific work is a product of a unique time and context. This is as true of this volume as it was of OWM I 1970. We therefore use this introductory chapter as a comparison between the two books to illustrate some of the paradigm shifts and (if we dare use the word) progress that has marked evolutionary primatology over the past three decades.

At the beginning of the 1970s, the cercopithecoid monkeys were, for many anthropologists, important as the "poor relations" of the hominoid primates in general, and the human species in particular. This teleological approach, derived from non-darwinian progessionism and ultimately from the pre-evolutionary *Scala Naturae*, had the effect of reducing the rich and internally varied cercopithecid radiation to a single rung on a ladder leading towards *Homo sapiens*. To some extent, it was exemplified by Adoph Schultz's contribution to OWM I, in which he stated that "under the skin" cercopithecoids were remarkably similar – a generalization which has been repeated many times since its original formulation.

As Cliff Jolly recalls, the inadequacy of the prevailing, one-dimensional view of the cercopithecids was brought home to John Napier during in his investigation of the early Miocene catarrhines, especially *Proconsul africanus* (now *P. hesloni*). At the time, discussions of the evolutionary position of *P. africanus* tended to focus upon whether it fell "above" or "below" the divide between cercopithecoid monkeys and their supposed ape descendants. To the extent that it was unlike the one, it was assumed that it should have resembled the other. In his investigation of its functional anatomy, however, Napier showed that (in many respects) *Proconsul* resembled neither group and was often closer to the larger platyrrhine monkeys. Contrary to expectation, the cercopithecoid monkeys were unsuitable models for early catarrhines because they showed a number of specialized (we would now say "derived") postcranial features that were neither primitive retentions, nor foreshadowed the developments seen in apes. Napier interpreted these features as a heritage from a common ancestor that was – unlike early apes – semi-terrestrial in its habits. This interpretation has stood the test of time remarkably well. The bilophodont molars of cercopithecids, though less unambiguously interpreted (see contribution by Brenda Benefit, Chapter 6), also pointed to ancestral cercopithecoid adaptations that were neither primitive nor ape-like.

Comparative studies of the cercopithecid postcranial skeleton and dento-facial complex also revealed a considerable internal diversity. The cercopithecids were not only the most widespread and successful of the extant catarrhine superfamilies, they showed a wide range of variation, much of it clearly related to function. The fossil record demonstrated that much of this diversity was the result of a late Neogene radiation that replaced that of *Proconsul* and similar catarrhines.

In both respects, therefore, cercopithecid monkeys appeared to be the successors of the hominoids, rather than their antecedents, and it was in the light of this conceptual change, and the interest that it generated about cercopithecid diversity, that the original Old World monkey conference and volume were conceived. As a logical organizing principle, the papers considering cercopithecoid diversity were focused upon the aim of producing a consensual classification of the group. The new approach seen in the 1970 volume – the study of cercopithecoids as interesting animals in their own right – was much more than simple taxonomic justice. In hindsight, we can see it as an early manifestation of an approach that was to become dominant later in the decade – a clade-based, "bushy" concept of organic diversity, in which major groups, including divisions of the order Primates, are

organized according to their derivation *from* a series of common ancestors, rather than by their approach *towards* an implied endpoint.

Although there are many continuities between OWM I and the present volume, there are also major differences resulting from the growth and development of primatology and related fields in the late twentieth century. It is no longer possible to invite a sizeable proportion of scientists working on cercopithecids to assemble around a single table. Nor can we insist that the full diversity of the taxon be included, though there is still a danger of bias because some genera are far better known than others.

We have designed the current volume to incorporate fields that did not exist 30 years ago (such as socioendocrinology) plus the approaches that reflect John and Prue Napier's own interests and are still valuable today. The volume is divided into two broad divisions. The first consists of chapters that deal with evolution, functional morphology, and systematics. The second focuses on social behavior, socioendocrinology, and ecology.

Evolution, morphology, and systematics of the Cercopithecoidea

A decade ago, Patterson (1987:1) wrote that,"To retrieve the history of life, to reconstruct the evolutionary tree is still the central aim of evolutionary biology." The authors of OWM I sought to achieve this goal by searching for a taxonomic scheme based upon multiple lines of evidence. At the time, both evolutionary taxonomists and pheneticists (the latter were not represented in the 1970 book) tended to emphasize that maximum accuracy and repeatability came from including as many uncorrelated traits (morphological, molecular, behavioral) as possible in a classification. In addition, the late 1960s and 1970s were the heady days of the multidisciplinary approach to evolutionary and ecological questions; a different scenario from the increasingly specialized biology of the past decade. A glance at OWM I also reveals that two major approaches of modern systematics – cladism and molecular techniques – had just begun to penetrate into the study of cercopithecoid history.

Molecular approaches

Patterson (1987:1) identifies the "oldest" and "newest" approaches toward the study of phylogeny, comparative morphology and molecular biology, and asks "Do molecules and morphology give the same picture, or two more or less distorted views of the same picture, or two quite different pictures?" In primatology, these questions date at least as far back as the

controversies surrounding Miocene hominoids – which were contemporaneous with OWM I.

Although Jukes (1966) had laid the basis for the field, molecular systematics was still in its infancy in 1970. It is a sign of the Napiers' farsightedness that they included two contributions from this field. One of these, by Barnicot and Wade (1970) presented a very preliminary analysis of hemoglobin polymorphisms and erythrocyte enzyme variation. While it was limited in its conclusions, it represented an approach that was used extensively in the study of primate population biology during the next 15 years.

Sarich (1970a) presented a general paper that focused on the value of molecular studies and embraced the neutral mutation explanation for the "regularity of protein evolution" (Sarich, 1970a: 23). This view was further expanded in his second contribution (Sarich, 1970b) and applied to a variety of primates. Indeed, Cliff Jolly recalls that the most animated discussion was of hominoid rather than Old World monkey data. Of Sarich's (1970b) specific conclusions, by far the least palatable to paleontologists was his insistence that the only reasonable interpretation of the evidence placed the human species nesting phylogenetically within the African great ape clade, probably next to the chimpanzee, and that immunological data made a great antiquity for the ape–human split improbable. Since 1970, this "troglodytian" conclusion has been so fully accepted that we often forget that this interpretation of the evidence (also espoused by the Huxley–Gregory–Washburn morphologically-based intellectual lineage) was only one of several competing scenarios. Sarich's (1968, 1971) positioning of the last common ancestor of humans and African apes at no more than four to five million years (Myr) competed strongly with the morphologically-based paradigm (Simons, 1972), which identified specific ancestors for hominids, the gorilla and the chimpanzee in the Miocene.

Sarich's (1970a,b) papers carried a more general, and more revolutionary, implication that had direct relevance to cercopithecoid systematics: that the power of molecular evidence so far outweighs that of morphology and behavior, that the most parsimonious strategy is to reconstruct phylogeny entirely from the biomolecules. This was explicitly stated when Sarich (1971:76) wrote that "the body of molecular evidence on the *Homo–Pan* relationship is sufficiently extensive so that one no longer has the option of considering a fossil specimen older than about eight million years as a hominid *no matter what it looks like.*" If this conclusion attacked the foundations of morphological study of hominoid evolution, which had received considerable attention, it could easily be extended to morphological study of the phylogeny of other primate families. Indeed, if both Sarich (1970a,b)

and Schultz (1970) were correct, then the morphological study of cerco-pithecoid evolution would be unproductive.

Sarich's (1970b) second contribution dealt more directly with issues of cercopithecoid phylogeny. After presenting an exposition of the immuno-logical method as applied to albumin, and of the validity of the molecular clock, Sarich presented a number of conclusions: catarrhines and platyr-rhines had diverged at no more than 35–40 Myr from a common "monkey-grade" ancestor; the cercopithecoid–hominoid divergence occurred about 22 million years ago (Ma); the colobine-cercopithecine split occurred at about 16 Ma; the divergence of *Nasalis and Pygathrix* took place at approx-imately 5 Ma; there was a "recent" common ancestor for all macaques; patas monkeys and vervets "share a common ancestral lineage subsequent to the divergence of the other species tested" (an affiliation that has received support from both Disotell, Chapter 2, and Groves, Chapter 4); and the drill and mandrill cluster together in contrast to *Papio* baboons and the gelada. Napier (1970) pointed out that some of these conclusions were con-trary to prevailing paleontologically-based ideas, for example, the separa-tion of colobines and cercopithecines in the late Oligocene or early Miocene.

Since 1970, molecular data relevant to phylogenetic resonstruction have increased enormously in diversity and information content, and interpreta-tions have become more sophisticated. Immunologically-based analyses of phenetic distance have been replaced by cladistic analyses based upon molecular sequences. Early enthusiasm for the molecular clock has been tempered by the realization that the evolution of particular proteins, and the DNA sequences that code for them, often varies from time to time, from taxon to taxon, and among loci (Avise, 1994; Strauss, 1999). This necessi-tates careful choice of the "timepiece" according to the problem at hand. Nevertheless, conclusions drawn from well-established molecular data are so widely accepted that they serve as a check on the wilder speculations of evolutionary biologists, and as an impetus to further molecular and morphological research.

Todd Disotell, in Chapter 2 exemplifies these new data and ideas, which he combines with a discussion and reanalysis of previously published infor-mation. His analysis produces reassuringly few inconsistencies, major sur-prises or deviations from the accepted, morphologically-based cercopithecoid phylogeny. A few contentious points, such as the phyletic position of *Nasalis* and the holophyly of groups such as the genus *Macaca*, the Asian colobines, and the African papionins, are resolved in favor of the traditional interpretation. The evidence of a special relationship between

patas and vervet monkeys, suggesting the removal of the latter from the genus *Cercopithecus*, is non-traditional and supports Groves's analysis of morphological data (1989; see also Chapter 4).

This consistency, however, throws the few apparent conflicts between morphology and molecules into sharper relief. Most notable of these is the paraphyly of both of the subgroups traditionally recognized among the African papionins; neither the *Papio*–gelada–mandrill cluster nor the mangabey genus *Cercocebus* is holophyletic. Baboons, geladas, and black mangabeys (separated as *Lophocebus*) form a clade that does not include the other genera, which may themselves form another, much older, clade. This unorthodox phylogeny is now supported by additional molecular data (Harris and Disotell, 1998), and by re-analysis of morphological features (Fleagle and McGraw, 1999).

Disotell emphasizes the need for a broader molecular database, and cautions against uncritical acceptance of single-locus phylogenies. Yet one cannot fail to be impressed, in hindsight, by how often such phylogenies have been supported as more robust sequence data become available. The analyses of electrophoretic patterns of hemoglobin and isozymes (Barnicot and Wade, 1970) and immunological similarity of albumins (Sarich, 1970b) are cases in point.

Population genetics

Today, virtually all "hands-on" field studies – and many that do not involve capture at all – can collect materials (blood, hair, faeces) from which genetic information can be derived. Ever since Darwin's (1859) formulation of natural selection as a primary evolutionary mechanism, and with the development of theoretical and quantitative population genetics, the notion of intra-populational diversity has been crucial to conceptualizations of evolutionary process at all levels. In the earlier decades of this century, theory was ahead of the technical means needed to measure genetic diversity in natural populations empirically. For cercopithecids, skeletal and dental biometrics provided virtually the only means of estimating natural diversity. Such data were linked to population genetic theory by the bridge provided by contemporary quantitative genetics. For population genetic models to be tested against nature, it was necessary to find appropriate Mendelian (and therefore countable) genetic markers and to survey them in real populations. By 1970, such work was being carried out (some of it by Nigel Barnicot and Cliff Jolly, participants in the conference) but none of it was included in OWM I.

Since the 1970s, several generations of genetic markers (simple, discrete, one-locus variants inherited in a Mendelian manner) have replaced each other as favorites of empirical population geneticists and have been used to analyze wild cercopithecid populations. This succession has been driven by three major considerations. One is ease of application (for example, isozyme electrophoresis is technically simpler and more easily interpreted than is immunological determination of erythrocyte antigens). A second is the power of the method as a population genetic tool, which is proportional to the amount of variation revealed (variable microsatellite loci, unlike polymorphic isozymes, are virtually unlimited in number and may have far more alleles per locus and higher heterozygosity than do isozyme loci).

A third, theoretically-driven, consideration is the selective neutrality of the variation. Models used to derive the effect size of breeding populations and subpopulations from the distribution of genetic diversity make the simplifying assumption that subpopulation differentiation is driven by a combination of mutation, genetic drift, and gene flow. Variation, neutral or not, is potentially subject to drift in any finite population, and drift is a particularly important evolutionary force in small populations. The context-specific action of natural selection on non-neutral variation is an unwelcome complication in applying real-world data to such models, and workers tend to make the simplifying assumption that the variation is neutral in regard to selection. The idea that most genetic variants are selectively neutral has a background in theoretical population genetics of the first half of the century (Wright, 1931) and received support (Harris, 1966; Lewontin and Hubby, 1966; Kimura, 1968; King and Jukes, 1969; Kimura and Ohta, 1971; Lewontin, 1974) at the time of OWM I. It was also a strong plank in the platform of advocates of a protein-based molecular clock driven by stochastic processes. However, because mutations recognizable by isozyme electrophoresis change the physico-chemical properties of an active protein, it is difficult to sustain the assumption of universal selective neutrality for such variation (Hudson, 1996; Fogleman *et al.*, 1998). For this reason, as well as ease of application, population geneticists have eagerly adopted techniques that carry the search for genetic variation to the level of the genetic material itself.

The contribution by Jeff Rogers (Chapter 3) illustrates the developments that have occurred since 1970, and discusses the use of the rich genetic data that can now be generated for natural populations. His study of genetic variation in yellow baboons of Mikumi, Tanzania, was the first on DNA-level variation in a natural cercopithecid population. He used restriction

fragment length polymorphism (RFLP) techniques to uncover variation in nuclear DNA sequences that are non-coding, and therefore assumed less likely to be directly influenced by natural selection. It is, however, quite possible for such loci to be influenced by selection upon coding sequences to which they are linked. Since the Mikumi study was completed, further technical developments – in which Jeff Rogers himself is a major participant – have led to the replacement of RFLP technology by a more prolific source of genetic markers, microsatellite analysis. Neither RFLP nor microsatellite variation can be shown to be universally neutral because proving the absence of selection is even more difficult than the converse. Such loci, however, are so numerous and widespread in the genome that it is in principle possible to distinguish those whose distribution is so far from the overall, stochastically driven pattern of variation as to suggest powerful selection on a linked locus, or on the microsatellite itself.

The most striking finding of Rogers' Mikumi study is that baboon populations carry high levels of intra-populational diversity, presumably because of universal male dispersal before breeding. This has important implications for modes of speciation in cercopithecines. Highly outbred populations are able to sustain a high frequency of normally unexpressed genes for recessive traits, often, but not universally, deleterious. Cliff Jolly argues that, if such a population is subdivided by habitat fragmentation, its subpopulations would be forced to inbreed and would have the potential for rapid (and not necessarily habitat-driven or "adaptive") evolutionary change and diversification as these genes are phenotypically expressed. Genetic tools that enable us to compare the population structure of species with wide and restricted distributions open the way to test alternative, theoretical models of speciation that are of particular relevance to the cercopithecoids, a speciose and comparatively young evolutionary radiation.

Morphology

In these days of emphasis on molecular approaches to the study of evolution, we often forget that early in the twentieth century Driesch (1908) could confidently assert that the study of morphology was at the "center" of biology. Nyhart (1995: 1–2) eloquently articulates the current attitude when she writes "Morphologists might be expected to sit among dusty museum cabinets, puzzling over mange-ridden specimens . . . while more progressive scientists uncovered the real secrets of nature in their laboratories." Yet, the study of morphology is more than a purely descriptive enter-

prise, since it is a field that continues to generate new paradigms and approaches to the study of evolution. Morphology not only remains a viable approach to the study of phylogeny (as evidenced by Groves, Chapter 4, and Maier, Chapter 5), and the most direct method of studying the history of the primates (see Benefit, Chapter 6, and Gundling and Hill, Chapter 7), it also provides information on rates (Gingerich, 1993) and pattern of evolution (Anderson, 1993; Leakey, 1993), ontogeny and size-shape relationships (Ravosa and Profant, Chapter 9), and function (Whitehead and Larson, 1994; Hiiemae, Chapter 8). The role and methodology of modern comparative anatomy has been discussed by Duncker (1985), Dullemeijer (1989), Gans (1989), and Riedl (1989).

The fields of comparative morphology, paleontology, and paleobiogeography were of professional interest to John Napier, and he wrote on each of these areas during his career. OWM I included a number of contributions in these "traditional" fields of primatology by Adolph Schultz, Elwyn Simons, Cliff Jolly, and John Napier.

The study of morphology in primatology has been revolutionized since the publication of OWM I by the introduction of cladistic methodology and philosophy, the application of experimental techniques to the study of function, and an increased emphasis on the study of size in functional and phylogenetic interpretations. Gans (1989) identifies phylogeny, ontogeny, size-shape, and function as the four basic "dimensions" of comparative morphology; all four areas are represented in this volume.

Cladistic systematics

At the time of publication of Napier and Napier (1970), few primatologists were aware of the basic principles and methodology of cladistics. The dominant paradigm was the less formalized "evolutionary systematics" that had grown out of the New Synthesis. Publications such as Simpson's (1961, 1963) and Mayr's (1969) were considered the standard texts on the philosophy and procedure of classification, and the major challenge to evolutionary systematics in the United States was phenetics (Sokal and Sneath, 1963).

Thorington's (1970) contribution to the original volume reflected the general view, when he characterized phenetic and cladistic classification as "useful." Mayr (1974) tended to be somewhat more critical. In fairness to the practitioners of primate classification at that time, it must be remembered that the population-based perspective of the New Synthesis was an important advance. Previously, some primatologists had erected new taxa on the basis of relatively minor morphological variation (e.g. Elliot, 1913),

and so there was an effort to bring the systematics of modern and fossil primates into the context of population variability. The contributions in Washburn's (1963) *Classification and Human Evolution* reiterate this point, and Simons and Pilbeam (1965) is an outstanding example of application of population thinking to the fossil record.

Hennig's system of classification was first articulated about 15 years before it was available in English (Hennig, 1950, 1965, 1966), and was not widely applied to primates until after the publication of OWM I. A paper that was specifically directed at cercopithecoid phylogeny was among the first to explicitly use cladistics; Delson (1975) is a classic because it details cladistic approaches, presents cladograms of the colobinae and papionini, and identifies ancestral morphotypes that have dominated the literature (see Benefit, Chapter 6).

The widespread use of cladistics changed not only the procedures used in erecting classifications, but also shifted the kinds of questions asked by primatologists and their paradigms of evolutionary change. For example, rather than focusing on the traditional question of ancestor–descendant relationships, often couched in an anagenetic paradigm, cladists now concentrated on the identification of sister-groups among taxa through the analysis of character states (Forey, 1992; Panchen, 1992). Simons (1970, 1974) exemplifies the older mind-set, when he attempts to draw a relationship between *Parapithecus* and cercopithecoids on the basis of similarity between a Fayum mandible and *Miopithecus talapoin*. This interpretation was later disputed (Delson and Andrews, 1975), and a cladistic perspective led to the suggestion that derived features in *Parapithecus* indicate ecological-functional convergence to cercopithecoids (Szalay and Delson, 1979).

Cladism not only signaled a formalization of systematic methodology, but also an emphasis on speciation (cladogenesis) rather than anagenetic change. Krishtalka (1993) discusses anagenetic versus punctuated models of Eocene primate evolution. This shift is logical, because the widespread application of cladistics has paralleled the rise of punctuated equilibrium as a dominant model of the tempo and pattern of evolution. Punctuated equilibrium was in the process of formulation (Eldredge, 1972; Eldredge and Gould, 1972) at the time of publication of OWM I. Paul Whitehead points out that a relation between cladism and punctuated equilibrium should be expected, since a close reading of Hennig (1966) reveals that many of the assumptions of punctuated equilibrium were already built into cladism. He would also argue, however, that it is unfortunate that there has been adherence to Mayr's (1942, 1963) model of peripatric speciation

(which is at the base of punctuated equilibrium). The idea that speciation has proceeded through the establishment of geographical barriers (Booth, 1958) and refugia (Hamilton, 1988) is not new in the study of cercopithecoid evolution and it has precluded testing of other models of speciation (e.g. parapatric speciation by Endler, 1977).

Groves (Chapter 4) presents two cladistic analyses. One analysis is of cercopithecid genera, using the Colobidae as an outgroup. Forty-six characters are used; they are a mixture of mainly dental and cranial traits, with a small number of other features. The study supports the ideas that *Lophocebus, Gorgopithecus, Dinopithecus and Parapapio* are papionines. He suggests that *M. nemestrina* may also be a papionine, but urges caution. Groves supports the notion that *Mandrillus* and *Cercocebus* are sister-groups. His other cladistic analysis is of the *Cercopithecus*-group, with *Allenopithecus* as the outgroup; 22 cranial and dental characters are used. He affirms a suggestion that he had made previously (Groves, 1989) that vervets should be separated from *Cercopithecus*, and that the genus *Chlorocebus* should be used for green monkeys instead. This conclusion is based on three skull characters that ally vervets with patas monkeys. He also concludes that *Allenopithecus* does not belong to the Cercopithecinae.

Maier's contribution applies a comparative morphogenetic approach to a little-studied anatomical area, the ethmoidal region. Studies of the ontogeny of morphological characters have a long history in vertebrate zoology (de Beer, 1937). Martin (1990: 127) writes that, "Developmental evidence provides one of the most powerful available aids for separating primitive from derived character states and every attempt should be made to include ontogenetic information." While some regions have been repeatedly studied in primates, such as browridges, others have been comparatively neglected. The ethmoid forms an anterior portion of the cranial cavity and portions of the medial orbital walls; it is perhaps most obviously characterized by its cribiform plate. Maier identifies characters in the ethmoidal and nasal regions that distinguish cercopithecoids, including a reduced ethmoturbinal recess and posterior nasal cupula, and a lack of a sphenoidal sinus. This analysis provides an important comparative study of primates in this region.

Paleontology

Evolutionary primatology has always had an emphasis on the discovery and description of fossils because of its close ties with the study of human evolution. Physical anthropologists have sought to discover specimens and

name new taxa, often in an attempt to discover hominid "ancestors."
Actually, it is somewhat surprising that a field that has emphasized fossils
has also wholeheartedly embraced cladism because many phylogenetic sys-
tematists (Patterson, 1981; Rosen *et al.*, 1981) de-emphasize the role of
fossils in determining evolutionary relationships. At the time of OWM I,
most primatologists would probably have agreed with Simpson (1961: 83)
that "fossils provide the soundest basis for evolutionary classification"
although Sarich had demonstrated that molecular techniques were begin-
ning to become important.

Despite this emphasis on fossils, it has only been in recent years that cer-
copithecoid paleontology has been viewed as more than a sideshow to
human evolution. This change has partially been due to the efforts of some
particularly active paleontologists, such as Eric Delson and Meave Leakey,
but also because of the variety of fossil monkeys. The Plio-Pleistocene
record has been especially interesting, with discovery of the terrestrial colo-
bine *Cercopithecoides* (Szalay and Delson, 1979), the large colobine
Paracolobus (Birchette, 1982), the large-bodied *Theropithecus oswaldi* and
new interpretations of its postcranial anatomy (Jolly, 1972; Whitehead,
1992) and evolution (Leakey, 1993), and the unique *Theropithecus brumpti*
(Eck and Jablonski, 1987). There has also been increased discovery and
study of Miocene cercopithecoids. Simons (1970: 104) was correct when he
stated that, "Until recently the Miocene monkeys of Africa have remained
largely undescribed, unnamed, or misidentified." While Miocene homi-
noids still receive the greatest amount of attention (Begun *et al.*, 1997),
there has been progress in our understanding of Miocene cercopithecoids
since von Koenigswald (1969).

Benefit's authoritative contribution (Chapter 6) demonstrates that fossils
are important for the elucidation of the ecological bases of adaptive radia-
tions, and that they still have potential for the determination of phylogeny.
Benefit reviews the evidence on the phylogenetic positions of Miocene
monkeys, and concludes that *Victoriapithecus* and *Prohylobates* belong to
the Victoriapithecidae rather than the Cercopithecidae. Her description of
the well-preserved *Victoripithecus* cranium is important in this regard. In
addition, this analysis contradicts the expectation that a colobine-like skull
was primitive for the cercopithecoids, an ancestral morphotype postulated
by Delson (1975). Benefit argues, contrary to the idea that fossils are of
little value, that "Incorporating the Miocene sister-taxa of modern homi-
noids and cercopithecoids into cladistic analyses is more appropriate for
determining morphocline polarities within each superfamily." Benefit's
analysis assumes that there is not much convergent evolution in the skull

nor dentition of Old World monkeys; convergence has, however, occurred in the postcrania of different groups of cercopithecoids (Whitehead, 1992).

Benefit then conducts an extensive dental comparison to illuminate the origins and significance of bilophodonty. She states that the molars of early and middle Miocene cercopithecoids were not adapted for leaf-eating, and that the origin of bilophodonty may be related to an increase in grinding area provided by increased occlusal surfaces of the hypoconulid and entoconid. She believes that early monkeys ate hard fruits and seeds, and discusses various models of the split between hominoids and cercopithecoids. The paleoecological evidence leads her to suggest that Miocene apes inhabited forest environments, while victoriapithecids lived in "drier, more unpredictable and open environments."

Benefit's anatomical and paleocological analysis is complemented by Gundling and Hill (Chapter 7) who summarize the geological data from fossil sites in eastern Africa. Geological evidence has been treated in an equivocal manner in these days of phylogenetic systematics. It has been argued that geological sequence is "a poor guide to the polarity of characters and the order of occurrence in time need not match the order of nodes in a cladogram" (Benton and Storrs, 1996: 32). This attitude is in direct contrast to that which prevailed during OWM I, when age of appearance was used as a ranking criterion in classifications. Yet, age and geological context are important in reconstructing paleoenvironments, which is crucial if explanations of adaptive contexts are to be formulated. At the least, morphologically-based cladograms and stratigraphic data may be tested against each other.

Gundling and Hill review the chronological age and paleoecological/taphonomic reconstruction for all major cercopithecoid sites, from the early Miocene through the Pleistocene. They make the point that the pattern of evolution of genera is different from that found in the New World, because modern Old World monkey genera appear recently in the late Pliocene and Pleistocene while many modern platyrrhine genera appear in the Miocene.

Allometry

The study of allometric scaling is the analysis of change in a body part relative to change in body size. As such, it is a valuable tool to help us to understand evolutionary changes in form and function. Body size is an important variable in understanding animal biology, from the level of tissues to trophic ecology. The relationship between size and physiology has been well-documented for many years. Since the late 1970s, there has been

increasing realization that size also matters for ecology (Peters, 1983) and evolution (Calder, 1984; Damuth and MacFadden, 1990). Important concepts, such as symmorphis, have originated from allometric investigations. Issues regarding the number of species present in the fossil record, as in the case of *Archaeopteryx* (Houck *et al.*, 1990), have been resolved by studies of growth series. Primates have received considerable attention because of the existence of substantial interspecific differences in body size within all families. Of course, the Hominoidea have tended to receive the most scrutiny. However, the Cercopithecoidea are also of considerable interest because they "exhibit marked diversity in adult cranial proportions and body size" (Ravosa and Profant, Chapter 9). Aside from questions dealing specifically with cercopithecoid phylogeny and function, body size should also elucidate the "role of ontogenetic and allometric factors in patterning morphological evolution."

Ravosa and Profant point out that allometric studies can help to differentiate functional convergence from close phylogenetic relationship. For example, colobines have relatively deeper mandibular bodies than do cercopithecines; but, so do large-bodied extinct papionins compared to other cercopithecines. This convergence can be functionally interpreted. In contrast, there appears to be a subfamilial difference in symphyseal robustness, with cercopithecines and colobines evolving in different directions. This type of approach was not utilized in OWM I.

Ontogenetic analyses of the cercopithecoid skull are also valuable, because they cause us to realize that "the shape of large (or older) individuals may depart significantly from that of smaller individuals only because the former have progressed farther along a growth curve that is strongly allometric" (Emerson and Bramble, 1993). Cercopithecoids have been the subject of intersexual and interspecific ontogenetic comparisons. Interspecific comparisons have implications for the study of phylogeny, since it is significant whether species show concordant or divergent allometric growth vectors. If scaling comparisons among species reveal divergent growth allometries, then this may indicate divergent adaptations; Ravosa and Profant discuss study of relative face length as a character in the formulation of cranial morphoclines, which has direct relevance to the disagreement between Delson (1975) and Benefit (Chapter 6).

Experimental functional anatomy

At the time of OWM I, experimental studies of vertebrate functional anatomy had begun on the masticatory apparatus (Crompton and Hiiemae, 1970). The experimental techniques of cineradiography and

electromyography are instrumental in determining the functional significance of particular anatomical features. Sometimes, results overturn long-cherished notions that were based on non-experimental anatomical deduction (Whitehead and Larson, 1994).

We are fortunate to have a contribution from one of the pioneers of experimental functional anatomy, Karen Hiiemae (Chapter 8). Hiiemae's work demonstrates that, despite anatomical differences in the orofacial complex, cercopithecoids and mammals from other Orders have the same three stages in their feeding process. However, cercopithecoids have the ability to chew, transport and swallow food at the same time; these activities occur in series in other mammals. In addition, the movements of the tongue and jaw are not as correlated in macaques as in other studied mammals. Hiiemae then speculates that these differences between monkeys and other mammals have implications for the evolution of human speech.

Socioendocrinology, social behavior, and ecology

Behavioral studies were represented at the 1969 conference by fieldworkers and a single zoo study. By implication, contemporary, experimental laboratory studies were considered too far removed from evolutionary concerns and naturalistic behavior to be worth including – the archetypical "monkey" of comparative psychology had little or no relevance to the theme of cercopithecid diversity.

Socioendocrinology

In the present volume, there are two contributions (see Chapters 10 and 11) representing the progress that has been made towards bridging the conceptual and theoretical gap between laboratory and field. Pat Whitten (Chapter 10) reviews the developing interface between naturalistic and experimental studies of behavior–endocrine interactions in monkey behavior. Since 1970, socioecology (the study of population- or species-specific adaptations of organisms in their naturalistic setting) has evolved into behavioral ecology, which incorporates some of the insights derived from sociobiological theory, and is less content to treat species adaptation as a self-explanatory consequence of evolution. Meanwhile, behavioral endocrinology, which traditionally treated the responses of organisms to experimental manipulation as though they were universal, or at least independent of the animal's individual and phyletic history, has given rise to socioendocrinology, which interprets the interaction between the behavior and

endocrine status of individuals within their social context. Whitten points out that these developments imply a convergence in methods and outlook, and looks forward to their further integration into evolutionary socioen-docrinology, which will seek to understand the evolutionary origins of species- or population-specific differences, as well as individual variation in behavior–endocrine systems. Such a synthesis must rest on knowledge of how hormones work in individuals (and recognition that endocrine–behav-ioral relationships are likely to be both two-way and non-linear); how the individual's genome is involved in the development of its behavioral pheno-type; and how individual physiology and behaviors give rise to the emergent features of a society, such as its group structure, philopatry patterns, and dominance hierarchy.

Similar themes emerge in Fred Bercovitch's (Chapter 11) consideration of the mechanisms and timing of reproductive maturation, and its inter- and intrapopulational correlates in cercopithecine monkeys. Though neces-sarily focused on baboons, macaques, and vervets, his review of the litera-ture shows that interaction between rates and patterns of reproductive maturation on the one hand, and nutritional, social, and ecological factors on the other is highly complex and variable from species to species and pop-ulation to population. Simplified models are poor predictors of behavior in group-living monkeys, since the choices open to individuals are limited by their social status and context. Some studies find dominant individuals of both sexes to grow faster and to reproduce earlier than their peers, but this is by no means universal. It seems that the advantage conferred by a domi-nant position in society does not lie in faster growth or earlier maturation *per se*, but rather in the freedom to fine-tune one's reproductive strategy in these respects. The relative freedom from social constraint enjoyed by dom-inant animals may provide them with a margin of time and energy that may be allocated tactically to rapid growth, or to reproductive maturation, or invested in social interaction. It any event, the complexity and subtlety of these interactions suggest that bivariate experimental designs, however appealing, are always likely to give conflicting and ambiguous results. Ultimately, interpretations will have to involve mechanisms at each of the levels of an integrated evolutionary socioendocrinology. As Whitten and Berkovitch both argue, the goal should be a synthetic behavioral primatol-ogy, in which levels of explanation, and effects working on different time-scales (immediate individual reactions; individual, ontogenetic development; emergent societal features; evolving species characteristics) are seen as interacting and mutually dependent, but also kept conceptually distinct.

The emphasis upon proximal mechanisms of physiological and genetic causation evident in both Whitten's and Berkovitch's reviews, recalls the work of Solly Zuckerman, whose primary subjects were cercopithecid monkeys. For many reasons, Zuckerman's views on the causes of primate sociality were almost universally discounted, even ridiculed, in the 1960s and early 1970s. This was a time when adaptation- and ecology-based ethology provided the predominant explanatory framework for naturalistic animal behavior (Crook, 1970; Kummer, 1971). The field-based and adaptation-oriented studies of baboons by DeVore (DeVore and Hall, 1965; Hall and DeVore, 1965) and Altmann and Altmann (1970) seemed to have shown that Zuckerman's (1932) observations of hamadryas baboons, the whole basis for his theory of causation of primate society, were quite wrong, the fatally flawed product of a hopelessly un-natural situation in the London Zoo. Also downplayed was Zuckerman's insistence that explanations lacking realistic proximal causation, rooted in established neurological and endocrinological mechanisms, had little more than metaphorical value. What could not be fully appreciated either by Zuckerman or his detractors was the extent of the inter-specific and interpopulational diversity in cercopithecid behavior that must be encompassed by any comprehensive explanatory scheme. As Whitten and Berkovitch show, there is ample scope for studying variation in a family that includes *Mandrillus*, with its unique hyper-polygyny and male "fatting"; cercopithecins with tight female kingroups and peripheral males; at least two variants of baboon social organization; and the several different social styles seen in species of *Macaca*. With so much still to do, premature generalization is a temptation to be avoided.

Social behavior and ecology

Ironically, a step towards the rehabilitation of Zuckerman's observations, and a demonstration of previously under-appreciated behavioral diversity, appeared in OWM I. Kummer (1971; Kummer *et al.*, 1970), reported that wild hamadryas baboons, like Zuckerman's Monkey Hill animals, lived in a society based upon male mate-jealousy, quite different from that of yellow and anubis baboons of Kenya. Kummer also reported the existence of a zone of natural hybridization between hamadryas and anubis baboons in central Ethiopia. The existence of this natural hybrid zone sparked a discussion of the nature of species, both in baboons and in general, that remained unresolved at the end of the conference, with the authors of the taxomomic summary (Colin Groves and Dick Thorington) each favoring a

different solution and nomenclature. The debate on the nature of species shows no sign of abating, and, indeed, may be intrinsically insoluble (Jolly, 1993), but continues to generate useful thoughts on the organization of nature.

Investigation of Kummer's hybrid zone also continues, and is the subject of the contribution by Jane Phillips-Conroy and her collaborators (Chapter 12). Phillips-Conroy *et al.*, document and discuss rates of dental attrition in wild baboons, and illustrate the dependence of such ontogenetic processes upon habitat features at a very local, population-specific level – a lesson that should be taken to heart by those using comparable data to interpret dietary habits among whole species or even genera of extinct primates. The fact that this study is based upon tooth-casts taken serially from wild animals exemplifies another way that laboratory and field techniques have been integrated since 1970. At that time, almost all primatologists, unlike other zoologists, strictly eschewed capture, marking, or other interaction with their subject animals, preferring a non-participant observer style. Kummer's work constituted a partial exception, combining field experiments, some on temporary captives, with traditional observation. In the further development of Kummer's project, Phillips-Conroy, Jolly, and their colleagues have developed a style of fieldwork in which hands-on methods are even more prominent; target populations of baboons (and grivet monkeys) are regularly trapped and re-trapped, as well as being subjected to naturalistic, non-intrusive observation before and after the trapping seasons. Similar methods have been gradually adopted by other fieldworkers, and are now almost routinely incorporated into programs of field study, even of highly arboreal species. Using materials that can be collected in such "hands-on" procedures, we are now able to base observational studies much more firmly upon a foundation of knowledge of the age, nutritional condition, health, population structure, and even the individual kinship, of the subject animals.

An obvious application of genetic information is in determining degrees of relatedness among individual animals interacting within a social system. Such data are needed to test propositions derived from a sociobiological explanatory framework, which emphasises the notion of natural selection as a consequence of differential individual reproduction, rather than a cause of species adaptation. The development of this theoretical orientation by Hamilton (1964), Wilson (1975), Trivers (1985), and their many followers, and its almost universal adoption as a working paradigm, undoubtedly represents the most profound change in behavioral interpretation since 1970. Moreover, cercopithecid monkeys are diurnal, live in per-

ennial social groups, and communicate largely by sensory channels shared by humans, all of which characteristics make them ideal subjects for the kind of detailed study needed to test sociobiological predictions.

The contribution by Lynn Fairbanks (Chapter 13) belongs within this tradition. It is a review designed to empirically test the prediction, drawn from parental investment theory, that mothers will continue to invest time and effort in their juvenile and adult offspring, to the extent that such behavior does not compromise the fitness of the mother herself. Necessarily based very largely upon macaques, baboons, and vervet monkeys, often in captive or semi-natural, provisioned, populations, the study finds that the behavior of mothers fits the predictions of "sociobiological rationality" quite well. The presence of a mother, especially a high-ranking one, is certainly beneficial, and the benefit extends to the next generation; a grandmother's presence benefits her daughters' offspring. But mothers invest far more in their infant offspring (to whom the care is far more vital) than in their juvenile and adult offspring, for whom peers – especially related peers – can be a major source of support. All this makes excellent sense, and provides further confirmation of the explanatory power of the sociobiological framework.

Along with the many insights that have derived from the sociobiological interpretation of primate social behavior, however, has come the risk of a new kind of inadvertent anthropomorphism, as Irwin Bernstein points out in his critical review (Chapter 14). Such interpretations are often expressed in a terminology drawn from human behavior, used as a kind of metaphorical shorthand. An over-literal interpretation of such language may lead to unwarranted assumptions. In particular, they may lead the unwary to assume an unproven level of sophistication in intentionality and cognitive processes on the part of the non-human actors, and obscure real and evolutionarily interesting differences in cognitive ability among non-human primates. The apparently limited ability of even the "smartest" of cercopithecids to learn new and potentially useful motor patterns by imitation from conspecifics, which apparently distinguishes them sharply from great apes and humans, is a case in point.

There is still much to be learned from empirical research of a more traditional kind on naturalistic behavior in the wild. Two chapters on African colobines lie within this methodological and theoretical framework, yet nothing comparable to them could have been written at the time of OWM I, because both rely upon data painstakingly gathered over many years from ecologically diverse sites, and treated comparatively. Tom Struhsaker (Chapter 15) examines patterns of intra- and inter-specific association in

African cercopithecoids, focusing on communities that include a popula-
tion of the "red" colobus (*Colobus badius*, s.l.). His conclusion is that the
threat of predation, especially by large forest eagles, is the strongest predic-
tor of polyspecific association in arboreal monkeys. However, considerable
variation is introduced into the overall picture by more diverse and local-
ized habitat factors that account for apparent exceptions, and patterns in
areas where eagles pose a lesser threat. If there is a general conclusion to be
drawn, it seems to be that an emergent feature of social organization such
as group size and composition, the product of a long and multifactorial
chain of social and ecological causation, is unlikely to be related in a simple
way to any single habitat variable.

John Oates, Carolyn Bocian, and Carl Terranova (Chapter 16) also draw
upon many years of fieldwork, and a rich theoretical background, as well as
the relatively sophisticated tools now available for digitally-based sound
analysis, in their discussion of differences in the acoustic structure of the
male loud calls of various populations within the black and white *Colobus*
group. Their interpretation demonstrates not only that species-groups
within the cluster can be distinguished by the properties of their loud calls,
but that these properties can be plausibly related to features of socioecol-
ogy that differ from species to species. Finally, the behavioral complexes of
which the loud calls are a component can be ordered along a polarity gradi-
ent of increasing specialization, providing a hypothesis of population
history that demands testing against genetic data.

In a contribution that is a model of meticulous analysis of painstakingly
gathered data, Marina Cords (Chapter 17) uses multi-year observations of
Cercopithecus mitis in a Kenyan forest, to examine relationships of domi-
nance among the females of a social group. For female blue monkeys, dom-
inance is apparently a low cost, low return proposition; the subjects showed
very low rates of agonisic interaction, and rank seemed to confer no mea-
surable benefit in terms of reproduction or access to resources. Yet when
they occurred, agonistic interactions indicated that the rank order among
individuals remained consistent over long periods of time. The obvious
inference is that the animals were retaining information that was rarely
reinforced or translated into overt behavior, yet was stable and presumably
important enough to be unambiguously expressed on the rare occasions
that it did emerge. Such observations should inspire humility in the prima-
tologist, reminding us that though all we can know about animal motiva-
tion comes from observation of behavior, it does not follow that observing
behavior can ever tell us all that is going on in the heads of our primate sub-
jects. Is the ability to retain a mental map of rarely expressed social relation-